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Deciding what to see: The role of intention and attention in the perception of apparent motion

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Abstract

Apparent motion is an illusory perception of movement that can be induced by alternating presentations of static objects. Already in Wertheimer's early investigation of the phenomenon [Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift fur Psychologie, 61*, 161–265], he mentions that voluntary attention can influence the way in which an ambiguous apparent motion display is perceived. But until now, few studies have investigated how strong the modulation of apparent motion through attention can be under different stimulus and task conditions. We used bistable motion quartets of two different sizes, where the perception of vertical and horizontal motion is equally likely. Eleven observers participated in two experiments. In Experiment 1, participants were instructed to either (a) hold the current movement direction as long as possible, (b) passively view the stimulus, or (c) switch the movement directions as quickly as possible. With the respective instructions, observers could almost double phase durations in (a) and more than halve durations in (c) relative to the passive condition. This modulation effect was stronger for the large quartets. In Experiment 2, observers' attention was diverted from the stimulus by a detection task at fixation while they still had to report their conscious perception. This manipulation prolonged dominance durations for up to 100%. The experiments reveal a high susceptibility of ambiguous apparent motion to attentional modulation. We discuss how feature- and space-based attention mechanisms might contribute to those effects.

Keywords: Attention; Apparent motion; Voluntary control; Psychophysics

1. Introduction

Apparent motion is an illusory perception of movement that is induced by a sequence of static displays (Roget, 1825). The phenomenon has been extensively studied in early 20th century psychology (DeSilva, 1928; Duncker, 1929; Kenkel, 1913; Korte, 1915; Neuhaus, 1930; Schiller, 1933) and was a central paradigm for the initiation of the Gestalt movement (Sekuler, 1996; Steinman, Pizlo, & Pizlo, 2000; Wertheimer, 1912). Already Wertheimer (1912), in his classic paper, reports the fact that an observer's focus of attention can significantly bias the perception of an ambiguous apparent motion display. According to his theory, spatial attention boosts processing at the attended location and thereby leads to faster processing times for the attended alternative, making it more likely to be perceived.

Since this time, there have been only few studies addressing the issue of attentional modulation of apparent motion. Ramachandran and Anstis (1983, 1985) mention that in their experiments with bistable apparent motion displays, observers were able to voluntarily control the perceived motion direction. They do not describe any quantitative measures for the amount of modulation but report that the influence breaks down when the apparent motion speed is increased (stimulus onset asynchronies below 350 ms). Suzuki and Peterson (2000) investigated another type of bistable apparent motion and found a multiplicative effect of intentional effort on perception: The more the stimulus itself was biased towards a certain interpretation, the more effective was the voluntary influence.

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The purpose of our study was to further investigate the extent of modulation by intention and attention for bistable apparent motion. We used the so-called 'motion quartet' (Hoeth, 1968; Neuhaus, 1930; Ramachandran & Anstis, 1983; Schiller, 1933), in which two pairs of dots at opposing corners of a virtual rectangle are presented in sequence so that either horizontal or vertical apparent motion can be perceived. The stimuli were presented in two different sizes in both experiments to see how modulation strength is affected by quartet size. In Experiment 1, observers were instructed to speed up and slow down percept changes in the motion quartet. The resulting percept durations were compared to a passive condition. In Experiment 2, spatial attention was diverted from the motion quartet with an attention-demanding detection task while participants still reported their conscious perception of the quartet. In this way, we were able to see how attentional focus affects the dynamics of bistable apparent motion.

2. Methods

2.1. Observers

Eleven members of the Frankfurt cognitive-neuroscience community (age, 21–33) participated in Experiments 1 and 2. Three additional participants were run in a control experiment. All observers had normal or corrected-to-normal vision. One participant was left-handed, all others right-handed.

2.2. Stimuli and apparatus

2.2.1. Experiment 1

Stimuli were generated with a custom-made program based on the Microsoft DirectX library and presented on a cathode-ray-tube monitor (Samsung SyncMaster 950P Plus). The distance between the participants' eyes and the monitor was 47 cm and the screen size 36.5 × 27.4 cm (field of view, 42.4° × 32.5° visual angle). The participant's position was fixed with a chin and forehead rest. The stimulus consisted of four circles (diameter, 1.7°) arranged as a virtual rectangle (Fig. 1). At any given time, only two dots at diagonally opposite corners were presented. A fixation cross (size, 0.3° × 0.3°) was always displayed in the middle of the screen. Stimuli had a Michelson contrast of 98% (luminance, 104 cd/m^2; background luminance, 0.81 cd/m^2). There were two versions of the motion quartet: (a) large, with a fixed horizontal distance between dots of 11° and a variable, observer-dependent vertical distance between 11° and 20.1°; (b) small, with a fixed horizontal distance between dots of 3.3° and a variable, observer-dependent vertical distance between 3.3° and 6.3°. Dots were presented for 150 ms with an interstimulus interval of 100 ms (2 Hz presentation frequency).

2.2.2. Experiment 2

The motion-quartet stimuli used in Experiment 2 were identical to Experiment 1 (large and small quartets). Instead of a fixation cross, participants looked at a character stream at the center of the screen (Fig. 1C). The stream consisted of alphanumeric characters (fixed height, 0.3°); the presentation frequency of the characters was 2 Hz and numeric characters appeared with a probability of $p = .125$.

2.2.3. Eye tracking

An infrared eye-tracking system (Ober2; Permobil Meditech, Timra, Sweden; Applied Science Laboratories, Bedford, MA, USA) was used to control for eye movements in three out of eleven participants. Eye movements were sampled at 500 Hz.

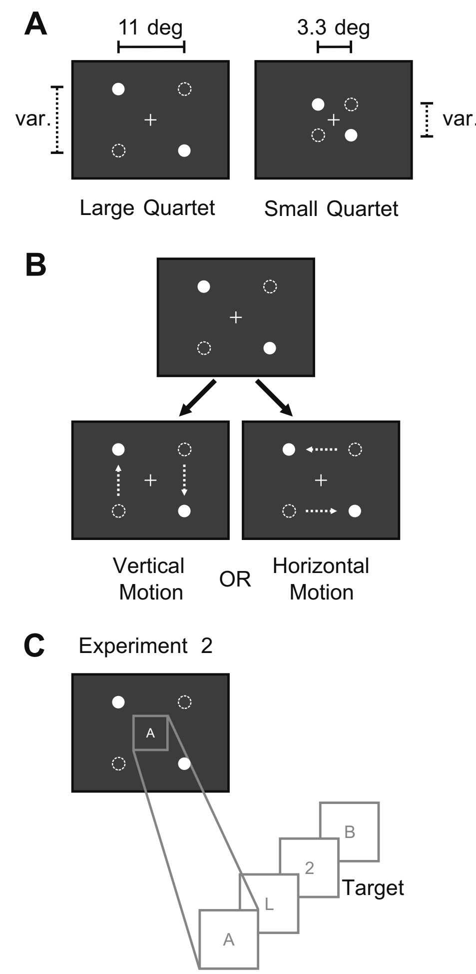

Fig. 1. Stimuli for Experiments 1 and 2. (A) For both experiments, large and small quartets were used. The horizontal distance was fixed and the vertical distance was adjusted for individual participants according to a preceding threshold measurement. The diagonally opposing pairs of dots (filled and dashed) were presented in alternation, leading to a percept of either vertical or horizontal motion (B). During prolonged viewing, the perceived motion direction oscillated between the two possible interpretations. (C) In Experiment 2, participants had to fixate a character stream in the middle of the screen instead of a fixation cross. During the Task condition, they had to detect and report the numerical characters among the sequence of letters.

2.3. Procedure

2.3.1. Threshold measurements

The optimal ratio between vertical and horizontal distance (aspect ratio) that leads to equal durations of vertical and horizontal motion perception can vary widely between observers. To get a balanced stimulus for every single participant, we used a 'Method of Limits' procedure to adjust the aspect ratio before the experiments began. The procedure was started by presenting a motion quartet with a very low aspect ratio (fixed horizontal distance, 6.6°; starting value for vertical distance, 4.4°) leading to unambiguous perception of vertical motion. The vertical distance was then ramped up and down in steps of 0.6° per 500 ms. Observers had to press a key when their perception switched between horizontal and vertical motion, which also reversed the direction of the step changes. Eleven percept reversals were recorded, the first value was discarded, and the average value of the remaining ten reversals was taken as the optimal aspect ratio for all following measurements. Participants were run in a test trial to familiarize them with the procedure before the actual threshold measurement was acquired.

2.3.2. Experiment 1

In the first experiment, participants received instructions to control the perceived direction in the motion-quartet stimulus. For every trial, they had one of three possible instructions: (i) "Try to alternate between vertical and horizontal perception as often as possible." (ii) "Passively observe the motion quartet." (iii) "At any time, try to hold the currently perceived motion direction. If the percept changes, try to hold the new perceived direction." Observers were instructed to report their perception (vertical/horizontal) by holding down one of two keys. If they didn't see any motion (motion breakdown), they were told to press no key. They were reminded to report their actual perception as veridically as possible, even when they had instructions to influence their perception. Most importantly, participants were instructed to keep steady fixation at any time. The combination of instructions (Switch/Passive/Hold) and stimulus size (large/small) resulted in six different conditions. Two trials each lasting two minutes were administered for each condition (12 trials overall). The trials were presented in two blocks (random sequence) with a one-minute break in between. Before the start of the actual experiment, observers were familiarized with the instructions and the stimuli in two test trials.

2.3.3. Experiment 2

In the second experiment, the stimulus display had a stream of alphanumeric characters instead of a fixation cross. Besides reporting the perceived motion direction of the motion quartet as in Experiment 1, observers had two possible additional instructions: (i) "Press a key when a numerical character is presented at fixation." (ii) "Press the key at random intervals, on average every four seconds." The first task was used to divert participants' attention from the motion quartet. The second instruction was employed as a control for any effects button presses might have on perceptual stability. In both conditions, participants were instructed to keep steady fixation on the alphanumerical character stream and report the changes in perceived motion direction as accurately as possible. Observers were familiarized with the attention–control task in a test trial. Two task types (attention task/passive viewing) and two stimulus sizes combine to four different trial types. Two trials were run per condition (eight trials overall). The trial sequence was randomly intermixed.

2.3.4. Control experiments

Three of 11 participants in the main experiment were measured with eye tracking. They wore goggles during the whole experiment. At the beginning and in the middle of the session, they had to perform additional calibration runs for the eye-movement analysis. We also measured an additional three subjects to control for the validity of subjective reports. For this purpose, three catch–trial periods (3 s) per run were inserted at random time points in the first, second, and third part of the run. Participants did not receive any instructions whatsoever concerning the catch–trial periods.

2.4. Data analysis

The durations of the individual percept phases (horizontal or vertical motion) were used as dependent variable. Phases with no motion perception were rare and discarded from the analysis. Also, the last phase of each trial was discarded, since the trial duration was fixed (2 min) and the last phase had therefore an arbitrary value. For each observer, phase durations were normalized to (divided by) the average phase duration in the passive condition, separately for small and large quartets. Statistical comparisons between conditions were performed with a repeated-measures multivariate analysis of variance (MANOVA) using the software package SPSS 12.0.1 (SPSS, Inc., Chicago, IL, United States of America). The distributions of phase durations were fitted with a gamma distribution (maximum-likelihood estimate) using Matlab 7.0.4.365 (The MathWorks, Inc., Natick, MA, United States of America). For the gamma fitting, data were normalized separately for conditions in each subject. To assess the correlations between subsequent phase durations, we performed lag-1 autocorrelations on phase-duration sequences, separately for observers and conditions. We then calculated a weighted average of the correlation coefficients across participants and tested for significance with an F statistic.

Eye-tracking data were analyzed with custom-made software using Matlab 7.0.4.365 (The MathWorks, Inc., Natick, MA, United States of America). Eye blinks were counted and eliminated by hand, and analyzed with non-parametric tests. The remaining data were detrended and transformed by an affine transformation derived from the calibration data and then visualized using fixation-density plots. For the eye-movement analysis, data were combined from large- and small-quartet trials.

3. Results

3.1. Threshold measurement

Before the experimental runs, we determined the optimal aspect ratio between vertical and horizontal distance for each participant with a ramping procedure. The optimal value for bistable apparent motion (50% vertical and 50% horizontal percept) can vary widely between observers (Selmes, Fulham, Finlay, Chorlton, & Manning, 1997; Sterzer & Kleinschmidt, 2005). In our sample the average aspect ratio was 1.45, ranging from 1.0 to 1.88 (Table 1). The threshold procedure was validated by calculating the ratio for the sum of vertical and horizontal phase durations as well as the ratio for the average vertical and horizontal phase durations. For both measures, the group values were around 1.0 in Experiment 1 (sum of durations, 1.08; average durations, 1.05), and around 0.9 in Experiment 2 (sum of durations, 0.91; average durations, 0.91).

3.2. Experiment 1

In Experiment 1, we tested the ability of our participants to voluntarily influence the perceived direction of movement in the ambiguous motion quartet. They were instructed to either (i) switch the percept as often as possible, (ii) passively view the percept, or (iii) hold the current percept as long as possible. Typically, the dynamics of perceptual alternations in multistable displays, such as binocular rivalry or the Necker cube, is characterized by gamma-distributed phase durations (but see Brascamp, van Ee, Pestman, & van den Berg, 2005) and low correlations between subsequent perceptual episodes (Lehky, 1988; Leopold & Logothetis, 1999; Muckli et al., 2002). In order to compare the perceptual dynamics of our stimulus to other paradigms and to assess the possible influence of the different conditions on the dynamics, we analyzed the distributions and autocorrelation functions in the different conditions. In all conditions, the distribution of phase durations could be well approximated by a gamma distribution (Fig. 2). When the fit was assessed with a Kolmogorov–Smirnov test, the distributions (large and small squares) for the Switch conditions were found to be significantly different from the estimated gamma distributions ($p << 0.001$). Note however that the degrees of freedom were not identical for the different conditions (see Fig. 2). In addition to the distribution of phase durations, we also analyzed the lag-1 autocorrelation of phase sequences. We calculated the correlation values in single participants (separately for conditions) and then derived a weighted group

Table 1
Threshold values for all participants ($N = 11$)

Participant	Pre	Exp. 1		Exp. 2	
	Aspect ratio	Ratio for sum of durations	Ratio for phase durations	Ratio for sum of durations	Ratio for phase durations
P1	1.12	1.52	1.38	0.93	1.09
P2	1.58	0.95	0.86	0.62	0.75
P3	1.48	0.91	0.90	0.41	0.28
P4	1.62	0.95	1.16	0.31	0.79
P5	1.57	0.84	0.87	1.10	1.02
P6	1.47	1.54	1.29	0.43	0.38
P7	1.17	1.14	1.11	1.16	0.87
P8	1.35	0.67	0.79	1.06	1.23
P9	1.88	1.18	1.14	1.13	0.87
P10	1.00	1.15	1.07	1.04	1.20
P11	1.68	1.06	0.94	1.85	1.51
Average	1.45	1.01	1.05	0.91	0.91

Notes. Pre, aspect ratio (vertical length of motion quartet divided by horizontal length) as determined in the threshold measurements. Exp. 1 and Exp. 2, ratios between vertical and horizontal values for sum of durations and phase durations. For optimal bistability, the ratio values should be 1.

mean of the correlation coefficients. For the Passive and Hold conditions, correlation coefficients were below .10 and non-significant ($p > .30$), similar to other multistable stimuli. In contrast, for both quartet sizes correlations between subsequent periods in the Switch condition were positive and significant: small quartet: $r = 17$, $F(1, 466) = 14.648$, $p < .001$; large quartet: $r = .23$, $F(1, 586) = 32.713$, $p < .001$.

For the small quartet, the average absolute phase duration for the Passive condition was 16.8 s (range, 8.3–41.0 s). The value for the Hold condition was 29.4 s (range, 15.4–77.5 s) and 8.5 s (range, 2.2–18.8 s) for the Switch condition. The respective values for the large quartet were Passive—17.5 s (range, 7.3–38.0 s); Hold—32.5 s (range, 12.8–98.0 s); Switch—7.2 s (range, 2.2–21.3 s). This indicates that participants were able to substantially increase and reduce phase durations. As can be seen from Fig. 3, this effect was present in every single observer. The group analysis was performed with a repeated-measures MANOVA on the normalized phase durations with the factors 'instruction' (Hold, Passive, Switch) and 'size' (small and large quartet). There was a significant effect for 'instruction' (Pillai's trace = .798, $F(2, 9) = 17.825$, $p < .001$), but no other effects reached significance ($p > .25$). With large

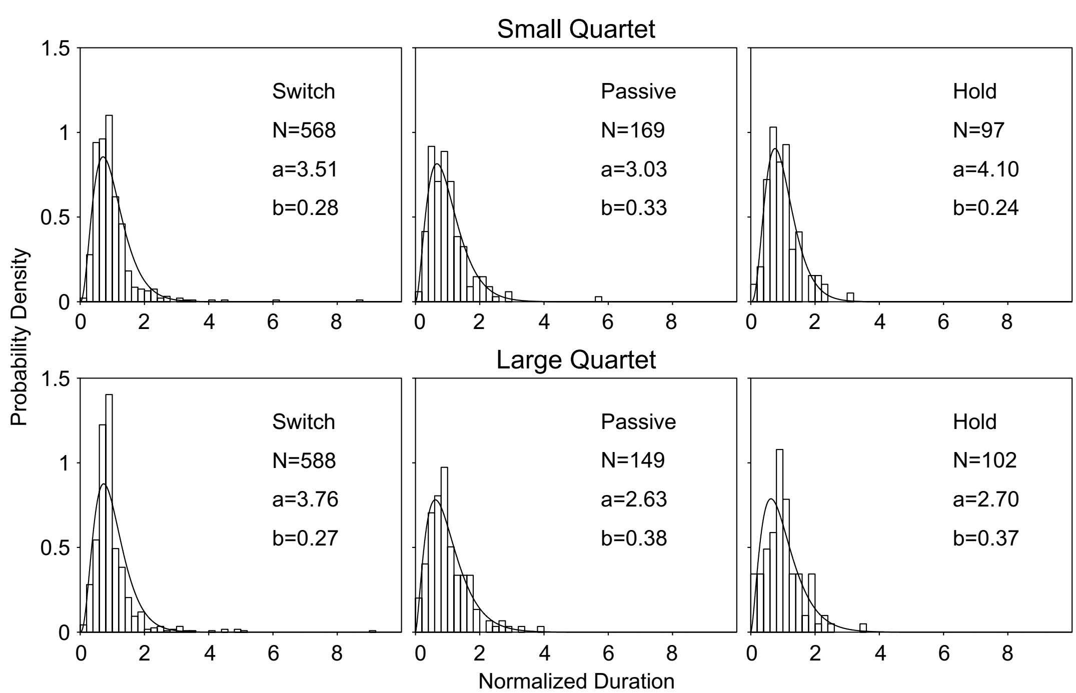

Fig. 2. Distributions of phase durations for Experiment 1. Histograms and best-fitting gamma distributions for all conditions and quartet sizes. For each participant, phase durations were normalized to the mean value in each condition separately. The parameters of the gamma distributions were calculated using maximum-likelihood estimates. N, total number of phase-duration samples from all participants; a, shape parameter of the fitted gamma distribution; b, scale parameter of the fitted gamma distribution.

quartets, phase durations in the Hold condition were increased by 92% relative to the Passive condition, the increase with small quartets was 83%. In the Switch condition, normalized phase durations were reduced by 58% with large quartets and only by 47% for small quartets.

3.3. Experiment 2

In Experiment 2, we wanted to probe the influence of spatial attention on the dynamics of percept changes. In psychophysical (Chaudhuri, 1990) and imaging studies (Murray & Wojciulik, 2004), it could be demonstrated that attention enhances adaptation of sensors. We wanted to test (a) whether the same holds true for bistable stimuli, (b) whether it is specific to the perceived direction, and (c) how strong the modulatory effect would be. To this end, we manipulated the focus of attention by a demanding detection task in the center of the screen (Task condition). Observers had to monitor a character stream and detect the numerical characters among letters (Chaudhuri, 1990). At the same time, they had to report the direction of motion in the motion quartet. In the Passive condition, observers had to maintain fixation on the same character stream but did not perform the detection task. To mimic the possible influence of button presses and for a minimal dual-task demand, participants had to randomly press the button used in the Task condition.

Data analysis was similar to Experiment 1. First, we assessed the dynamics of perceptual changes for the different conditions. Again all distributions could be fit with a gamma function (Kolmogorov–Smirnov test, $p > .25$), but the distributions in the Task condition deviated qualitatively from the typical pattern (see Fig. 4). In terms of the autocorrelation functions, no significant lag-1 correlations between phases were found in any condition ($p > .10$). The absolute mean phase durations for the Task condition were 40.8 s (range, 20.3–106.5 s; small quartet) and 41.8 s (range, 16.3–119.0 s; large quartet). In the Passive condition, the respective values were 34.7 s (range, 11.2–67.0 s) and 29.8 s (range, 11.5–108.5 s). For Experiment 2, the average phase durations in the Passive condition were longer than for Experiment 1, which might be due to the button-press task and the character stream at fixation. The normalized durations were analyzed using a repeated-measures MANOVA with factors 'instruction' (Task and Passive) and 'size' (small and large quartet, Fig. 5). The only significant effect was found for 'instruction' (Pillai's trace = .363, $F(1, 10) = 5.697$, $p = .038$). The effects for 'size' and the interaction were non-significant ($p > .10$). Also in Experiment 2, the modulation strength was descriptively greater for the large than the small quartets (1.97 vs. 1.46 normalized phase durations). This difference did not reach significance due to high inter-individual variance of results in Experiment 2 (see Fig. 5).

3.4. Control experiments

Experiments on bistable perception rely on observers' subjective reports for the quantification of percept durations. When participants have explicit instructions to modify their conscious perception (Experiment 1), it is possible that they deviate from veridical reports to conform to task demands. Also, in dual-task conditions (Experiment 2), observers could be sufficiently distracted to miss switches in conscious perception. To control for these factors, we measured three participants in runs where periods of unambiguous motion would occasionally occur. Observers were not informed about the manipulation and only received the usual instructions for the respective conditions. Two of the observers rarely missed any of the

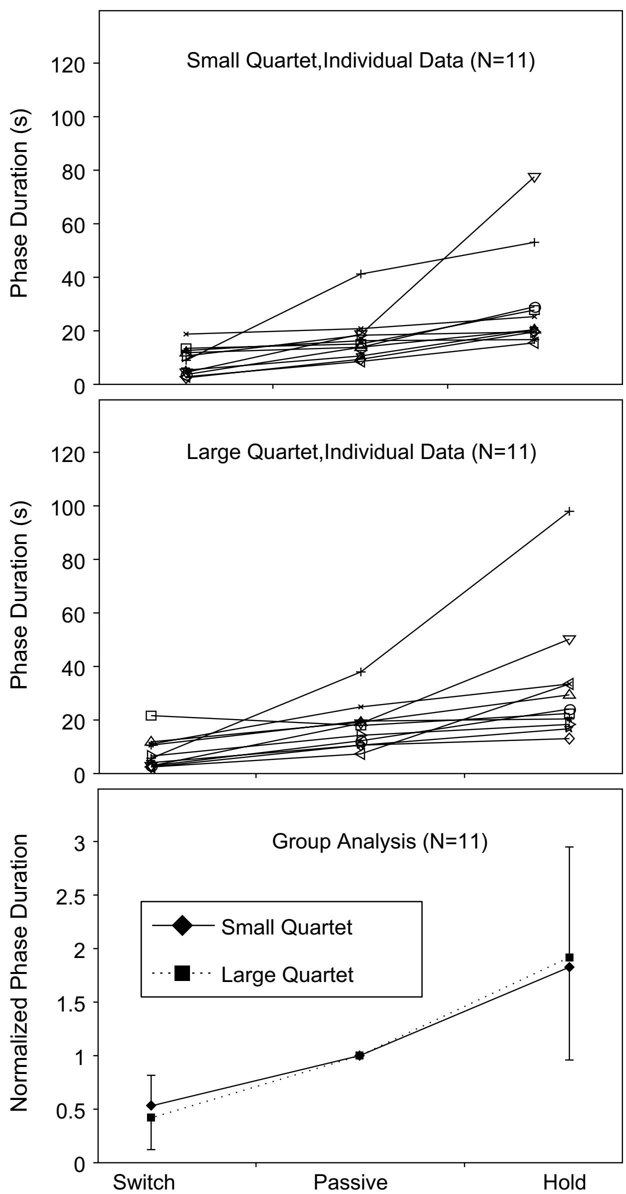

Fig. 3. Individual and group results for Experiment 1. Results for individual participants separated by quartet size (upper two panels). Group results across eleven observers (lower panel). In the group analysis, phase durations were normalized to the mean value in the passive condition for each participant. Error bars denote standard deviations across participants.

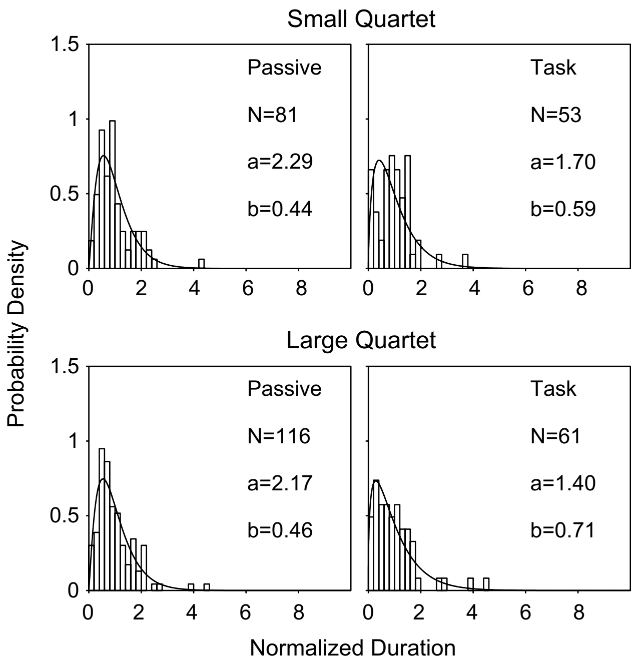

Fig. 4. Distributions of phase durations for Experiment 2. Histograms and best-fitting gamma distributions for all conditions and quartet sizes. For each participant, phase durations were normalized to the mean value in each condition separately. The parameters of the gamma distributions were calculated using maximum-likelihood estimates. N, total number of phase-duration samples from all participants; a, shape parameter of the fitted gamma distribution; b, scale parameter of the fitted gamma distribution.

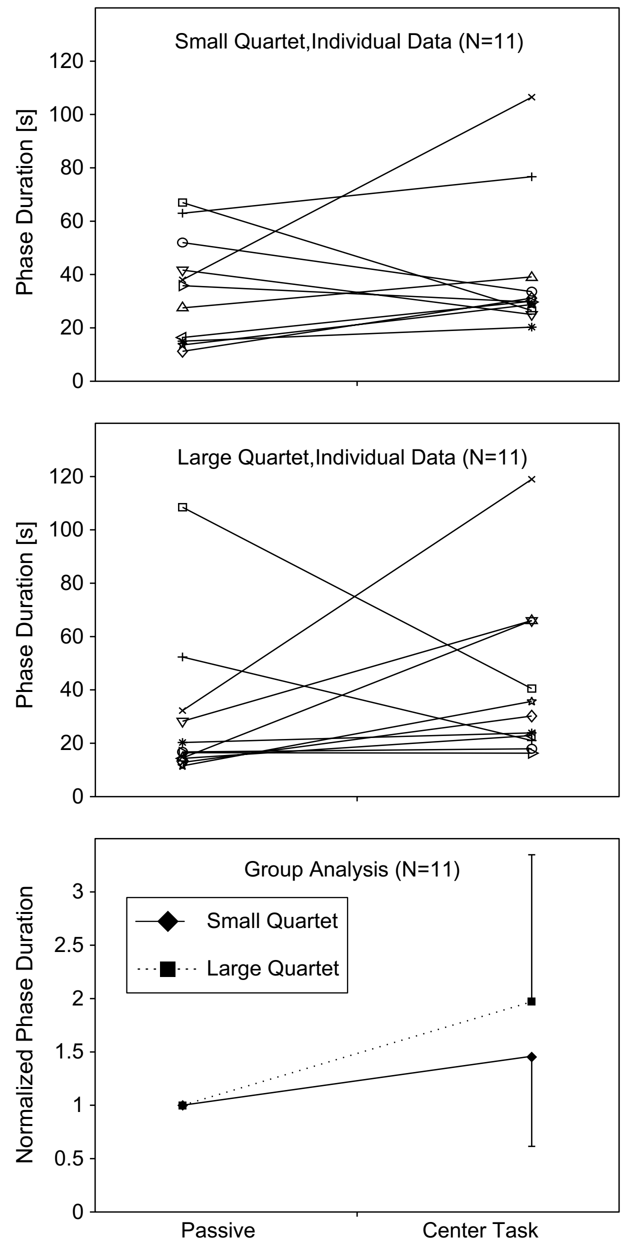

Fig. 5. Individual and group results for Experiment 2. Results for individual participants separated by quartet size (upper two panels). Group results across eleven observers (lower panel). In the group analysis, phase durations were normalized to the mean value in the passive condition for each participant. Error bars denote standard deviations across participants.

catch trials and there was no significant difference between conditions in both experiments ($p > .9$). The third participant had a substantial amount of errors, but, again, there was no apparent difference between conditions ($p > .7$). This confirms that our results can neither be explained by task demand alone nor by misses under dual-task conditions.

Another confounding factor that could influence perceptual switches differentially with respect to the different tasks is eye movements. We tracked eye movements in three participants of the main experiment. Blinks were identified by inspection and analyzed separately with a chi-square test. None of the observers showed any significant difference between conditions in both experiments for the number of blinks ($p > .25$). The blink-corrected data were also plotted to look for deviations in fixation patterns (Figs. 6 and 7). Surprisingly, the only apparent difference was that fixation was more focused for the Switch condition in Experiment 1. Therefore, the increased number of perceptual transitions in the Switch condition cannot be explained by a concomitant increase in eye movements.

4. Discussion

In our experiments, we investigated the effect of voluntary control (Experiment 1) and attentional focus (Experiment 2) on the perceived direction of movement in the ambiguous motion quartet. We also tested the influence of distance/eccentricity of stimuli on the modulation magnitude. Observers' ability to influence their movement percept was substantial. With the corresponding instructions, they could almost double (Hold) and more than halve (Switch) the phase durations for horizontal/vertical motion. This effect was descriptively stronger for the large compared to the small quartets. A comparable modulation effect—at least in magnitude—was found in Experiment 2, where in one condition observers had to perform an attention-demanding center task while tracking perceived movement of the motion

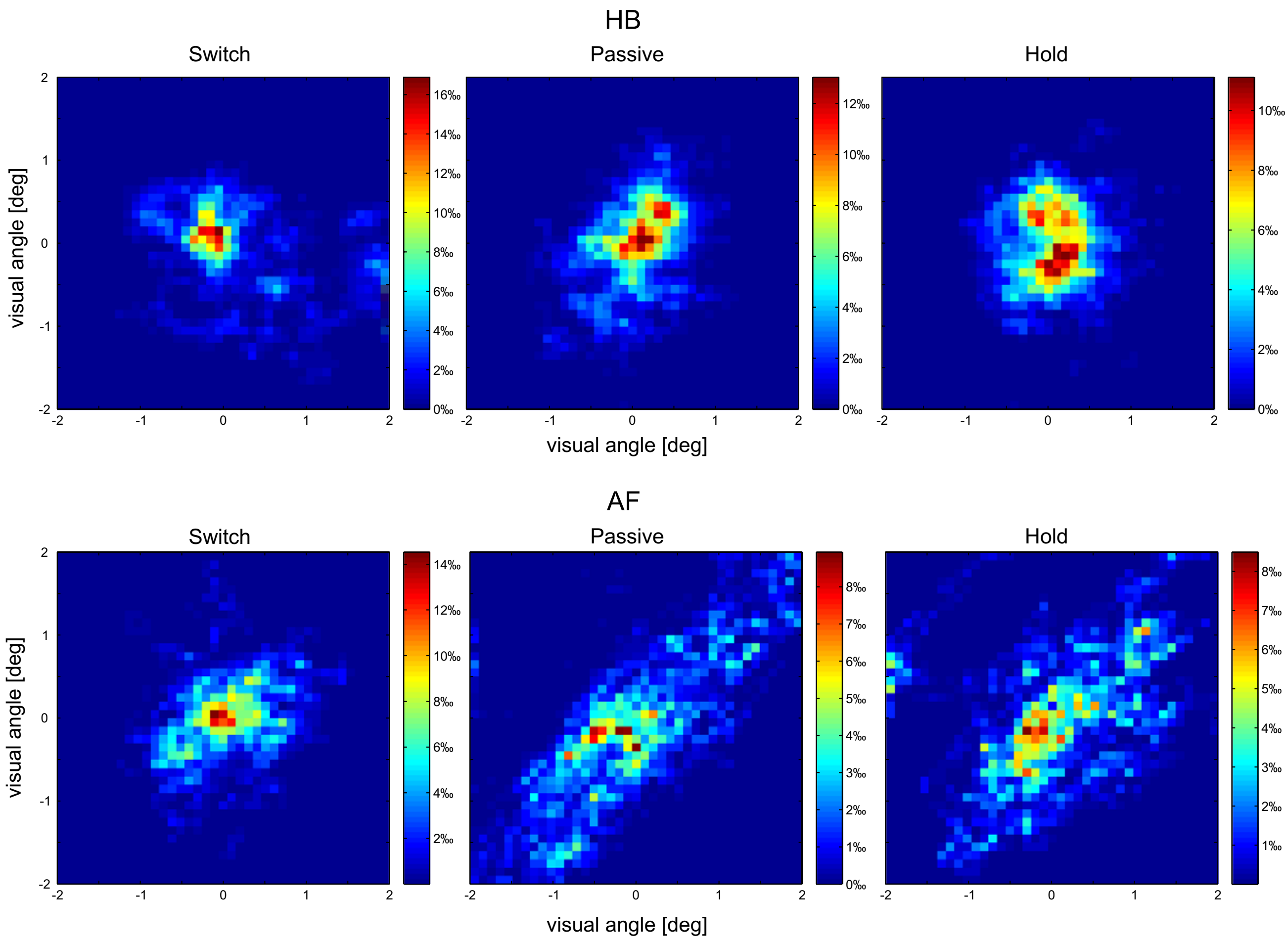

Fig. 6. Eye-Movement Analysis for Experiment 1. Fixation density plots for two observers in three conditions of Experiment 1. Data were collapsed across large and small quartets. It is evident that participant were well able to hold fixation during experimental sessions. Fixation was most focused for the Switch condition.

quartet. Through this manipulation, percept durations were increased by up to 100%. The effect was again descriptively stronger for the large quartet, but there was a large amount of variance across participants.

The dynamics of perceptual alternations for both experiments were comparable to other multistable phenomena. Most of the distributions were well fit by a gamma distribution and in almost all cases correlation coefficients were small and non-significant. There were two notable exceptions: (a) In the Switch condition of Experiment 1, the correlations between subsequent phase durations were significant with a medium-to-small effect size. This cannot be due to differences between participants since we calculated the correlation coefficients individually and then performed a weighted average. During the experiments, observers reported the Switch condition to be the most demanding one of all conditions because it required a lot of effort to constantly try to change the movement direction against the prepotent tendency of the percept to stay constant immediately after a switch. It is possible that observers' vigilance and effort drifted or oscillated slowly over the duration of a two-minute trial, which would lead to a positive correlation between subsequent percept durations. Alternatively, participants became more effective in manipulating their conscious perception and therefore showed a drift across trial duration. (b) Percept durations for multistable phenomena are supposed to be gamma-distributed (Leopold & Logothetis, 1999; Levelt, 1967). In most conditions, our data sets showed a good fit to the gamma distribution, although we cannot rule out that other functions provide an even better fit, as suggested by Brascamp and colleagues (2005). Only the distributions for the Switch condition in Experiment 1 were significantly different from the corresponding gamma fit.

In a previous study, Ramachandran and Anstis (1985) reported that their observers were able to intentionally manipulate the movement direction in a quartet display, but only when the stimulus-onset asynchrony (SOA) was above 350 ms. The SOA in our experiments was 250 ms, but, as reported, our participants showed a very strong control over their conscious perception. The reason for this difference might be that the distance between dots (more than 3° visual angle) and also the dot size (1.7°) in our stimulus was much larger than in the study of Ramachandran

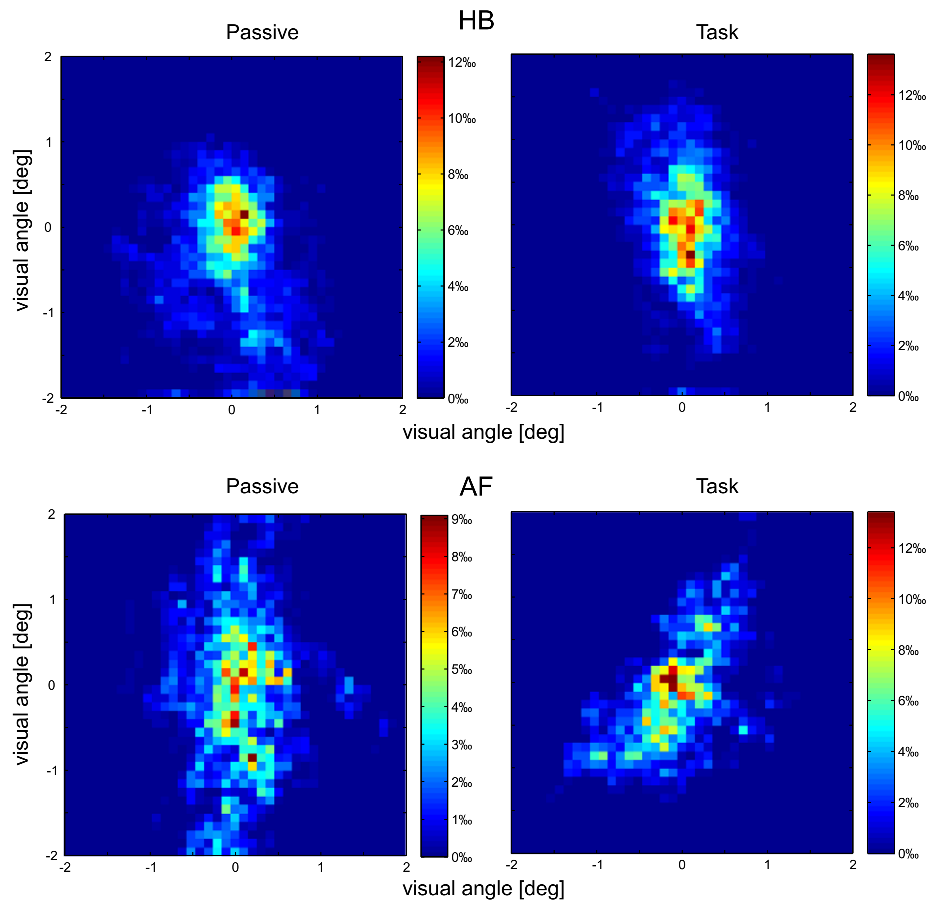

Fig. 7. Eye-Movement Analysis for Experiment 2. Fixation density plots for two observers in two conditions of Experiment 2. Data were collapsed across large and small quartets.

and Anstis. The distance between dots in their displays was 40 min of arc and the dot size 3 min of arc; these values are near the parameter range reported for short-range apparent motion displays (Braddick, 1980). Therefore, it is possible that there are qualitative differences between stimuli with different distances and dot sizes. We explicitly tested the scaling of voluntary control with distance between dots and found an enhancement of control, which did not reach statistical significance.

A recurrent concern in the investigation of multistable displays is the systematic influence of eye movements. This issue has been extensively studied for binocular rivalry (Blake, Fox, & McIntyre, 1971; Lack, 1971), where it has been shown that percept alternations do not exclusively depend on eye movements. But it is still possible that eye movements play a significant role, especially when participants receive explicit instructions to control their conscious perception. In a recent series of experiments, van Dam and van Ee (2006) meticulously investigated the relationship between perceptual alternations and eye movements in different perceptual-rivalry as well as binocular-rivalry paradigms. They found that there was a positive correlation between percept changes and saccades in binocular rivalry but not for perceptual rivalry (Necker cube and slant rivalry). Notably, this pattern did not change when observers had explicit instructions to influence their percept, suggesting that voluntary control is not exerted through saccades. We explicitly controlled eye movements in our experiments and are able to confirm previous results that voluntary control of perceptual switches cannot be explained by differential eye-movement patterns.

There has been a recent resurgence of interest in the amount of voluntary control and the influence of spatial attention on rivaling stimuli (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; van Ee, 2005; van Ee, van Dam, & Brouwer, 2005), especially binocular rivalry but also other types of perceptual rivalry. Meng and Tong (2004) compared the amount of control for different types of binocular rivalry and the Necker cube. They could show that voluntary selection of one of two possible percepts is well possible with the Necker cube but not with binocular rivalry. The modulation strength was about 40% for the Necker cube and only 10% for binocular rivalry. In addition, they tested non-selective control of the bistable stimuli, i.e., a non-specific increase or decrease in alternation rate. In this case, for both stimulus types they found a strong influence on alternation rates, especially for the speed-up of percept switches; the effect for the Necker cube was comparable to the results we found in Experiment 1, the effect for binocular rivalry was weaker. A major difference to our experiment was that participants in Meng and Tong's study could slow down the alternation rate of the Necker cube and binocular rivalry only by about 30%, whereas our participants could almost double phase durations in the Hold condition of Experiment 1. Similar results to those of Meng and Tong were reported by van Ee and colleagues (van Ee, 2005; van Ee et al., 2005). In addition to the Necker cube and binocular rivalry, they also investigated the recently developed 'slant rivalry' paradigm (van Ee, van Dam, & Erkelens, 2002), where the interpretation of depth structure is ambiguously determined either by perspective cues or disparity. Interestingly, slant rivalry showed the highest susceptibility to control and also had the longest dominance durations during passive viewing (about 6 s). Our stimulus has even longer natural dominance durations (about 20–30 s) and could easily be controlled voluntarily. It is possible that longer natural dominance durations facilitate the exertion of voluntary control, although this factor cannot exhaustively determine the degree of modulation. For example, the Necker cube has about the same natural dominance duration as binocular rivalry but is much more prone to selective influence.

In a series of experiments, Chong and colleagues could show that, under specific conditions, the selective effects of attention on binocular rivalry can be substantial (Chong & Blake, 2006; Chong et al., 2005). They found an increase of dominance durations of up to 80% when participants were engaged in an attention-demanding task on one of the rivaling targets (Chong et al., 2005). This modulation could be mimicked by increasing the contrast for the stimulus of interest during its dominance phases, suggesting that attention does in fact enhance perceived contrast, as has been suggested by other studies (Carrasco, Ling, & Read, 2004). They argue that the task is a necessary prerequisite for the effect of attention and explains the differences to the other studies described above, in which participants were only instructed to manipulate their conscious perception. What implications do the data of Chong and colleagues have for our results? Is it possible that the voluntary control of the motion quartet found in Experiment 1 and the attentional modulation of Experiment 2 rely on the same mechanism of contrast enhancement through attention? This is unlikely given the following arguments: (a) Observers could enhance as well as reduce dominance durations in Experiment 1, whereas in Chong et al.'s study attention only enhanced the duration of the attended percept. (b) The mechanism would have to act selectively on a specific motion direction. If one assumes that only the contrast of the inducing stimuli can be enhanced, this would be insufficient since the inducers are part of all possible stimulus interpretations. (c) The mechanism of Chong et al. cannot apply to Experiment 2. There we found an effect that was exactly opposite to what one would expect from a contrast–enhancement mechanism. When attention was drawn away from the stimulus, percept durations were significantly increased. Therefore, stimulus representations were actually weaker when attention was directed towards the motion quartet. This implies that quite different mechanisms are at play in ambiguous apparent motion and binocular rivalry.

So what are possible explanations for the effects of voluntary control and attention on the perception of the motion quartet? In Experiment 1, observers were able to change or hold their perception of movement with a high degree of control. It has been shown in electrophysiological (Martínez-Trujillo & Treue, 2002; Treue & Martínez-Trujillo, 1999; Treue & Maunsell, 1996) and imaging studies (Beauchamp, Cox, & DeYoe, 1997; Muckli, Kohler, Kriegeskorte, & Singer, 2005; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Rees, Frith, & Lavie, 1997; Saenz, Buracas, & Boynton, 2002) that neuronal activity can be influenced substantially by the attentional focus of observers. Especially the electrode recordings by Treue and colleagues in the macaque monkey could establish that not only observers' spatial focus of attention has an influence but that there are also specific effects for certain motion directions, which could be confirmed for humans in psychophysical (Alais & Blake, 1999) and imaging experiments (Saenz et al., 2002; Serences & Boynton, 2007). This means that we are able to selectively boost the representation of a certain direction of movement in a stimulus, comparable to the effect of spatial attention on stimuli presented at a certain location. This bias would be expected to be especially effective in determining conscious perception when a stimulus is ambiguous with respect to movement direction, as it is the case for the motion quartet. Slight increases in representation strength for one direction would tip the balance towards the intended percept. This effect might be especially strong for motion, since motion-processing areas show the highest degrees of attentional modulation (Muckli et al., 2005; O'Craven et al., 1997). Prefrontal cortex and possibly parietal areas might be the target structures responsible for the control of spontaneous and voluntary switches (Sterzer & Kleinschmidt, 2007; Windmann, Wehrmann, Calabrese, & Güntürkün, 2006).

In Experiment 2, percept durations were increased by up to 100% on average when observers had to perform an attention-demanding task at fixation. A similar effect has been described for the motion aftereffect (Chaudhuri, 1990). In this study, the same center task as in our experiment was used to divert observers' attention from an adapting unidirectional motion stimulus. Compared to the passive-viewing condition, the duration of the following motion aftereffect was considerably reduced with the attention task, a result also confirmed in later studies (Georgiades & Harris, 2000, 2002a, 2002b; Lankheet & Verstraten, 1995; Rezec, Krekelberg, & Dobkins, 2004). Although the exact neuronal mechanisms of the motion aftereffect are not known yet (Culham et al., 1999; Huk, Ress, & Heeger, 2001; Tootell et al., 1995; for a review see Anstis, Verstraten, & Mather, 1998), it is widely assumed that adaptation of direction-selective cells is the underlying cause. Adaptation processes have also often been adduced as explanation for percept changes in ambiguous apparent motion (Anstis, Giaschi, & Cogan, 1985; Clatworthy & Frisby, 1973; Finlay & von Grünau, 1987; Muckli et al., 2002; Selmes et al., 1997). For our results, this would imply that phase durations are prolonged by the attention task because adaptation for the perceived motion direction is reduced and therefore it takes more time to sufficiently reduce the strength of the dominant percept for a switch to occur. An alternative to the adaptation model has been proposed by Hock and colleagues (Hock, Schöner, & Hochstein, 1996). In their experiments, they found that adaptation might have a minor influence on perceptual switches in ambiguous apparent motion, but that the main causing factor is spontaneous activity fluctuations that can randomly tip the balance towards one percept or the other. On their account, a possible explanation for our results would be that diverting attention from the motion quartet in our experiments reduces the variance of spontaneous fluctuations and thereby leads, on average, to extended dominance durations.

In conclusion, we found substantial modulation of conscious perception of the motion quartet in a large sample of observers when they were instructed to voluntarily control motion direction. Moreover, a comparably large effect was observed when their spatial attention was drawn away from the motion quartet. Voluntary control might be achieved through feature-selective attentional mechanisms that boost one stimulus interpretation over the alternative. The effect of spatial attention can be explained by modulation of adaptation processes. When attention is drawn away, adaptation to the currently perceived motion direction is reduced, prolonging the phase duration of the dominant percept.

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